

MAPPING TERRITORIES WITH PLAYBACK: AN ACCURATE CENSUS METHOD FOR SONGBIRDS

J. BRUCE FALLS¹

ABSTRACT.—A playback method for mapping territories of songbirds is described, including suggestions for overcoming commonly encountered difficulties. Because birds are stimulated to sing and only boundary points are determined, this technique is more efficient for a single species than methods based on observation. Territory determinations are accurate in dense populations but may be unrealistically large where birds have no close neighbors and may follow a speaker into unoccupied areas. As a census method, about 5–15 birds in a 10–15 ha plot can be mapped with a single pass through the area in one morning.

Mapping methods of censusing breeding birds involve the enumeration of territories and the assignment of space to each singing male. Behavioral studies of territoriality often require more detailed maps. Since 1955, my students and I have mapped territories of several passerines using playback of recorded song. Similar methods have been used by Dhont (1966) and Krebs (1971). Here I describe our method, list our main findings concerning territorial behavior, and evaluate the usefulness of this technique for censusing songbirds.

METHODS

Traditional observational methods require repeated passes through surveyed plots or following individual birds for extended periods. Although territories are defined as defended areas, these methods only occasionally record instances of active defense. Most of the "points" gathered represent singing or foraging and, since these activities typically show marked central tendencies (Zach and Falls 1978, 1979) few boundary locations are obtained. Mapping the extent of defended areas in this way is a slow business.

We use playback of conspecific song to provoke territory holders into active defense and attempt to draw them to the boundaries of their territories. The method is relatively efficient because little time is wasted on interior locations.

We start near a singing bird which typically responds by calling, approaching rapidly, flying about the loudspeaker, and singing. In short, the territory holder responds as it would to an intruder. As soon as a bird approaches we move the speaker. Continuing in one direction, a point is soon reached where the bird will no longer approach, although a neighbor may do so. This establishes a point on the boundary of the original bird, either where it approached most closely or (more conservatively) at the last location where it sang. Alternatively, a boundary may be drawn midway between points of closest approach or song of two neighbors. Continuing with the original bird, the speaker may be taken back into its territory and moved as before but in a different direction. Thus, we follow a zig-zag path with locations inside and outside

the territory until we have mapped the defended area of one bird. Some information will have been gathered on neighboring birds and we can then explore their other boundaries. The rapidity of mapping depends on the responsiveness of the birds and the accuracy desired. With territories in the order of 1 ha, about 1 h per bird usually suffices (Fig. 1).

PROBLEMS AND SUGGESTIONS

Some birds do not respond readily and others lose interest rapidly. A few simple precautions help to minimize these difficulties. Songs of strange individuals (recorded some distance away) evoke the strongest responses (Weeden and Falls 1959). They should be played at normal volume which will require a recorder at high level if played directly from a Uher recorder. Intervals between songs used for playback should simulate a bird singing rapidly (say about 10 sec). Birds that do not respond initially often do so when a neighbor is attracted to a common boundary; thus, they can be mapped along with a more responsive neighbor. However, failing this, a visit on a later day may be necessary to fill in a "hole." Some birds (including recently banded ones) may not readily approach an observer. In dealing with such individuals (and for detailed mapping generally) it may be useful to place the speaker away from the observer on a long cable (say 20 m). Once a bird has responded, it will usually continue to do so if the speaker is moved quickly, playing only as many songs as are needed at each location. If a bird's response wanes it may be revived by using a different song. Unless a neighbor appears, the speaker should be taken some criterion distance (say 20–30 m) beyond the last point where a bird approached. To be sure that a bird which stops responding has not simply habituated to the playback, the speaker should be moved back to a point where it responded before. This can be done before moving off in another direction.

Confusion may result if several birds approach the speaker at once. On such occasions it helps to have more than one observer. First, any pairs should be identified. Beyond that, it is often possible to separate the voices of different individuals by ear. The different singers can be recorded using a small cassette recorder and identified later from "voice prints" (sonagrams). Problems of this kind arise along boundaries and can be resolved as the mapping proceeds. Sometimes neighbors invade each other's territories in pursuit of the playback. Usually, they are chased out again and a point of equilibrium is soon reached which can be

¹ Department of Zoology, University of Toronto, Toronto Ontario, M5S 1A1 Canada.

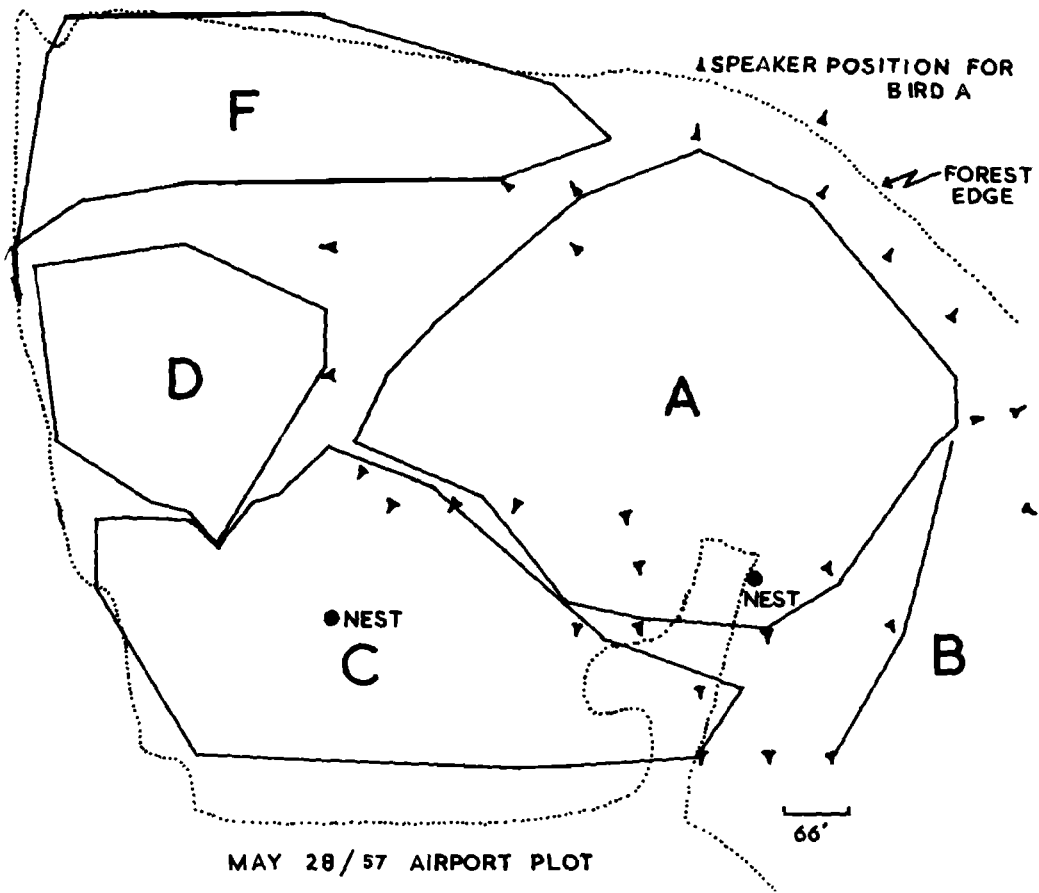


FIGURE 1. Territories of Ovenbirds determined in one morning using playback. (Speaker positions used for bird A are shown. Boundaries are based on closest approach.)

mapped as a common territory boundary. If these problems are severe, they may be alleviated by mapping each bird using its own song. Most birds respond fairly strongly to their own songs, while neighbors tend to ignore them (Weeden and Falls 1959).

Since responses wane over long periods, it is not advisable to return to the same area for several days. Indeed, the best map may be obtained on the first occasion so it pays to choose a day early in the breeding season, after territories have been established and when there is frequent song. Although mapping by playback can be done at any time of day, the morning is usually best. Rainy or windy weather should be avoided. As with other mapping methods, a grid of marked points is helpful and locations should be entered on a corresponding chart as the work proceeds. We have also used overlays on aerial photographs but even then some points of reference are needed.

EQUIPMENT

We use Uher (Report/Monitor) portable tape recorders, either directly or with a portable 10W amplifier and speaker (either Nagra DH Amplifier-Speaker or an amplifier with a separate mid-range horn). For

easy changing, tapes are mounted in Cousino Audio-vendor cartridges, held in place by electrical tape.

SPECIES AND HABITATS

Most of our mapping with playback has been done with three species: the Savannah Sparrow (*Passerculus sandwichensis*) which lives in rough grassland, the White-throated Sparrow (*Zonotrichia albicollis*) a bird of coniferous woodland and forest edge, and the Ovenbird (*Seiurus aurocapillus*) which only occurs in closed canopy forest. Our main study areas are in Algonquin Park, Ontario.

RESULTS AND DISCUSSION

RESULTS CONCERNING TERRITORIAL BEHAVIOR

(1) Birds respond strongly to playback, apparently attempting to evict the intruder. This is consistent with the notion that song is partly a threat display (Falls 1978) and with the concept of territories as defended areas.

(2) At any one time, the birds we have studied defend non-overlapping "song territories." Like

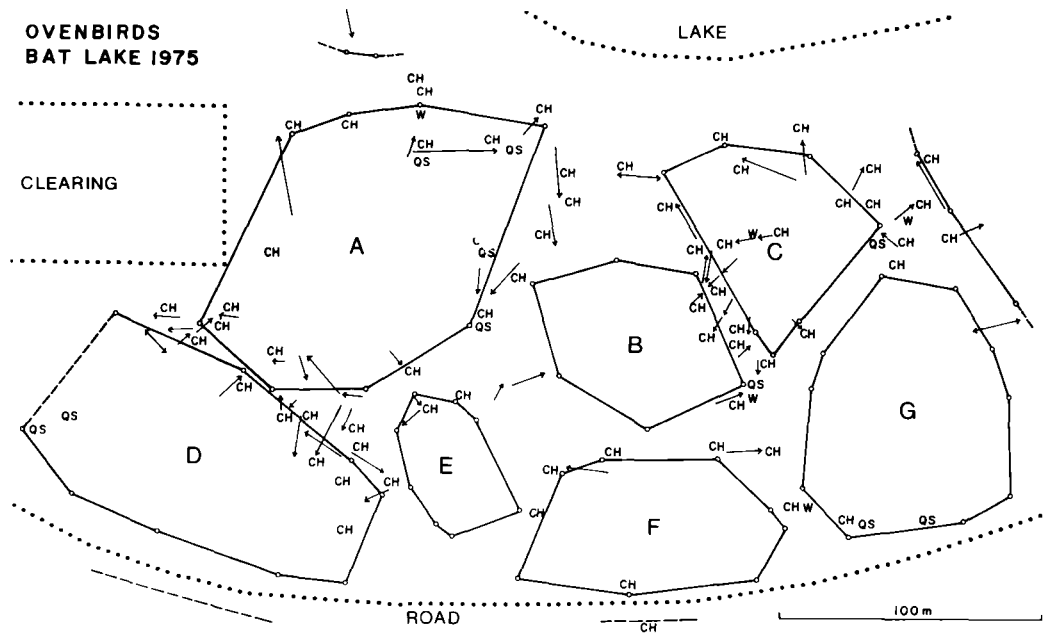


FIGURE 2. Ovenbird Territories determined over three mornings using playback. (Boundaries are based on closest song. Locations of chipping (CH), quiet song (QS) and warbling song (W) are also shown.)

other methods based on song, ours does not detect movements of silent birds beyond their defended boundaries. Thus, territory maps may not reflect the distribution of activities unrelated to defense (Zach and Falls 1979, Jones and Falls, MS).

(3) Neighbors may be separated by a narrow "buffer strip" in which they will not sing but may approach a speaker (Fig. 2). This suggests that they refrain from provoking each other, although they will still attack a strange singer in this area.

(4) Playback territories are usually larger than those determined by observation in comparable periods of time (day or season) (Figs. 3 and 4). This reflects both the greater efficiency of the playback method and a tendency for birds to attempt to defend larger areas than those in which they normally sing.

(5) Where birds lack close neighbors (in sparse populations, patchy habitats), they may follow a speaker into unoccupied areas giving extremely large estimates of territory size. For example, Savannah Sparrows occupying a narrow strip of rough grass beside an airport runway, followed speakers across the runway or into shrubbery where there were no other birds (Fig. 4, Table 1). We have obtained similar results with Ovenbirds. At Churchill, Manitoba, where White-throated Sparrows are scarce, a bird fol-

lowed a speaker for a mile. Clearly, in such cases territory measurements are unrealistic. However, these and similar observations show that an intruder will be challenged even where song territories appear to be widely spaced. Territory boundaries do not exist in a vacuum but are defined by points of equilibrium between intrusion and defense (Melemis and Falls, MS).

(6) Observation territories are usually contained within playback territories but boundaries obtained by the two methods may overlap (Fig. 4). This may result from shifting over time (different days), from boundary changes in response to playback, or from wandering beyond defended boundaries.

(7) When playback results are accumulated over a long period, adjacent territories often appear to overlap (Fig. 3). This reflects shifting of boundaries over time. Nevertheless, some territories remain very stable (Fig. 5). Playback territories of Ovenbirds do not seem to fluctuate in size with the breeding cycle as do areas in which birds sing spontaneously (Stenger and Falls 1959).

PLAYBACK AS A CENSUS METHOD

For censusing, the playback method can be speeded up by relaxing the accuracy of mapping. Thus, the recorder can be hand held and used directly and fewer boundary points (four to six)

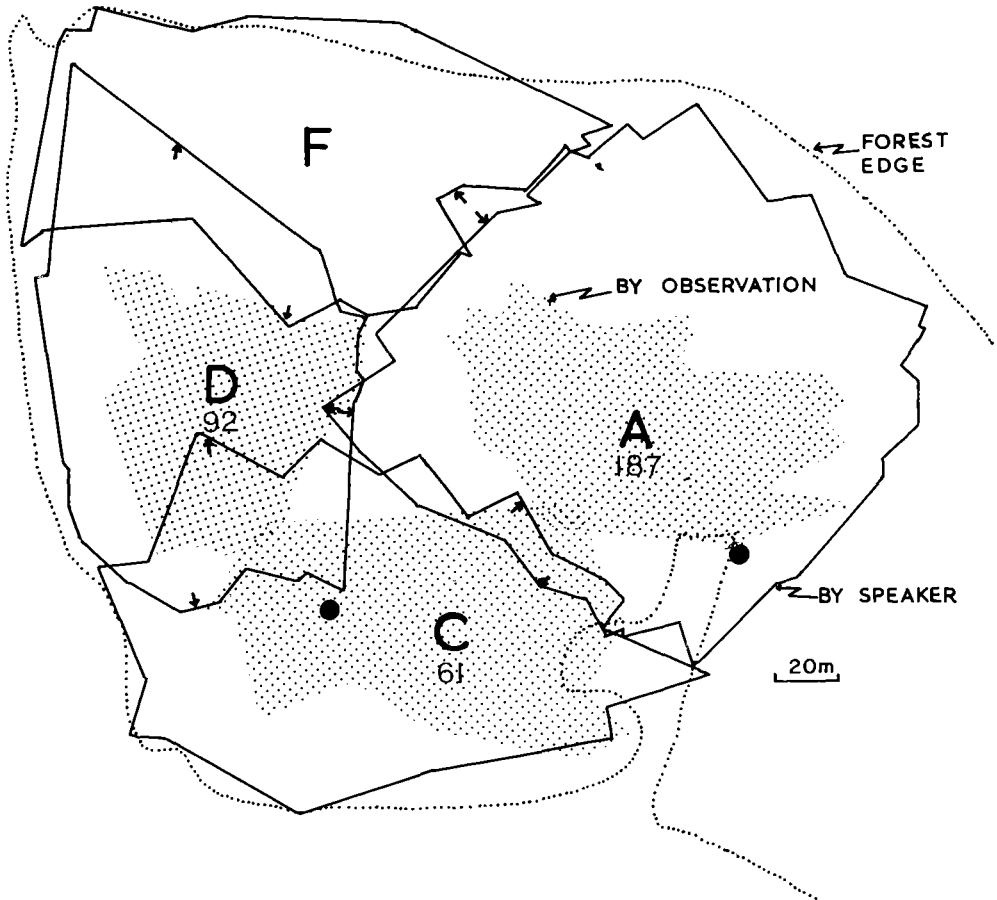
OVENBIRDS
AIRPORT 1957

FIGURE 3. Total Territories mapped by playback over the breeding season for Ovenbirds in Fig. 1. (Note smaller stippled areas obtained by observation for three birds and overlaps of playback territories.)

can be determined for each territory. We have been able to map (census) 5–15 males in 10–15 ha plots in one morning (Fig. 6).

The essence of this method is to account for the birds in all the occupied ground. The tendency (referred to above) of birds to defend unoccupied areas may pose problems for density estimation depending on two things: the amount of unoccupied ground and the size of the plot. In dense populations (little unoccupied ground) this should not be a problem. However, if the population is sparse (rare species, patchy habitat) there may be considerable movement of birds and the population could be overestimated if sample plots are small in relation to this movement. Since this is an edge effect it can be minimized by using larger plots. Thus, while play-

back helps to locate rare species, discretion must be used in interpreting territorial maps and estimating density in such cases.

The usefulness of playback for censusing is not confined to songbirds. The method described here should be applicable to any species using sound signals to advertise exclusive territories that are accessible to the investigator. Where these conditions are not met (less territorial species, inaccessible habitats) variants of this method may still be useful alone or in conjunction with other census techniques.

In cases where it works well, the following points summarize the features of this technique as compared with other mapping methods:

(1) Only one species can be censused at a time.

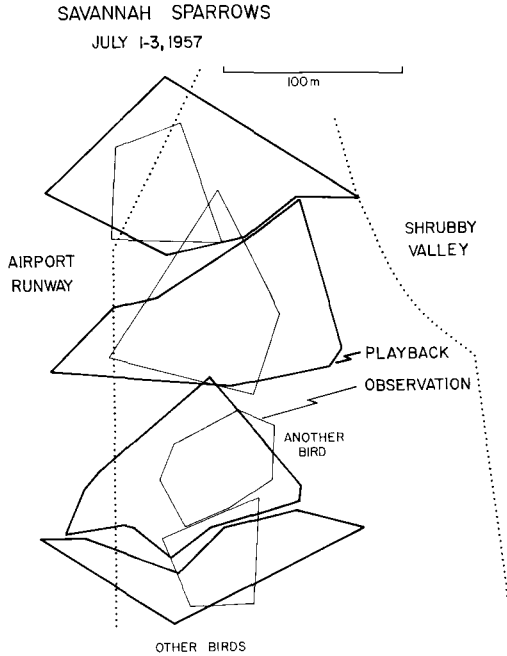


FIGURE 4. Territories of Savannah Sparrows determined over three mornings by playback (speaker) and by observation (overlaps on different days). (Birds followed the speaker into unoccupied areas at right angles to runway.)

(2) Usually a single pass through the area is required. Taking (1) and (2) together, the time required to census a few common species is comparable to that needed for other mapping methods.

(3) Birds that might not sing spontaneously during a census can be stimulated to do so. For

TABLE 1
DIMENSIONS OF SAVANNAH SPARROW TERRITORIES^a
AT RIGHT ANGLES AND PARALLEL TO AN AIRPORT
RUNWAY, DETERMINED BY TWO METHODS

(1) Bird	Observation method			Playback method		
	(2) Right angle to runway	(3) Par- allel to runway	(4) Ratio (2)/(3)	(5) Right angle to runway	(6) Par- allel to runway	(7) Ratio (5)/(6)
A	78	79	0.98	152	118	1.29
B	71	70	1.01	149	73	2.04
C	69	54	1.29	141	52	2.71
E	76	72	1.06	214	99	2.15
All	(3) > (4) in 11/20			(5) > (6) in 12/13		

^a Average of three to five trials per bird in meters. Figure 4 shows a typical trial.

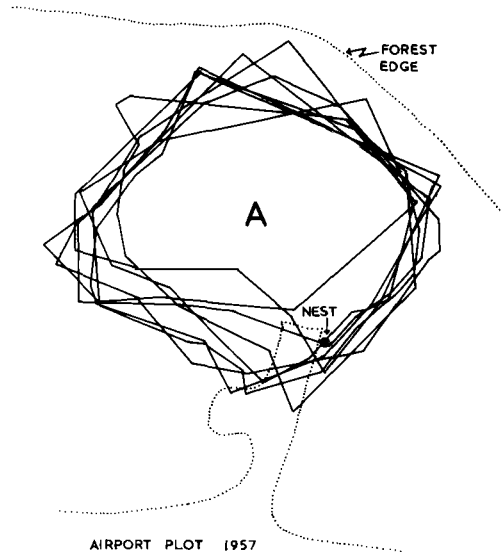


FIGURE 5. Territory Maps determined by playback for Ovenbird A in Fig. 1 over 8 weeks. (Note enlargement, to include the nest in later weeks.)

example, we have been able to census two morphs of the White-throated Sparrow which have very different rates of singing (Table 2). Members of the tan-striped morph would almost certainly be overlooked by observational mapping methods.

(4) Since birds are attracted to the vicinity of the observer, they can be heard and, if desired, recorded easily. Taking (3) and (4) together, problems of cue production and detection are minimized.

(5) Boundaries are obtained rather than clusters of points. This eliminates some problems of interpretation encountered in mapping methods based on observation.

(6) Because birds are stimulated to sing, this method is less sensitive than observational

TABLE 2
PAIRS OF WHITE-THROATED SPARROWS^a DURING AN
INSECT OUTBREAK, CLASSIFIED BY THE MORPH OF
THE MALE

Year	WS ^b	TS ^b	Total	% Change ^c
1969	12	6	18	0
1970	10	8	18	0
1971	12	12	24	33.3
1972	15	14	29	61.1
1973	17	10	27	50.0

^a Camp Road plot, Algonquin Park, Ontario.

^b Male morph: WS = white-striped, TS = tan-striped.

^c 1969 as base (= 18 pairs).

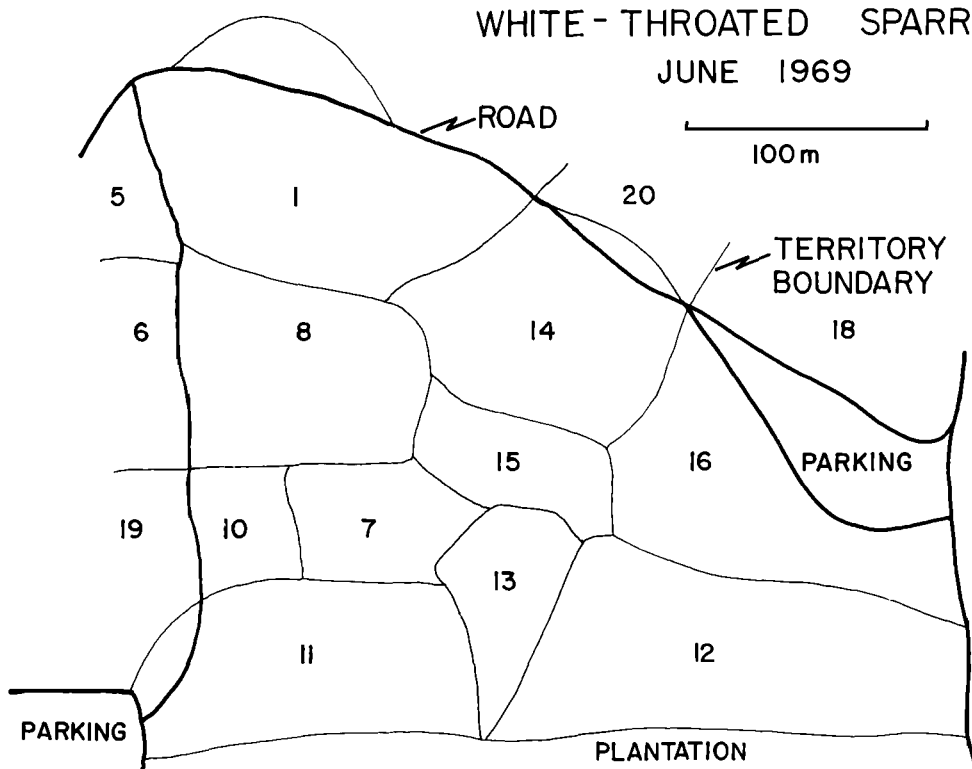


FIGURE 6. Census of White-throated Sparrows by playback in one morning. (Boundaries are drawn between points of closest approach by neighbors.)

methods to daily or seasonal effects. Thus, censusing need not be confined to the early morning or to the early part of the breeding cycle.

(7) In dense populations, we can check that all territorial birds have been counted by accounting for occupancy of all the ground. In such cases reasonable estimates of territory sizes are also obtained. This method does not, of course, enumerate non-territorial members of the population.

(8) Because playback can provide a total count of territorial birds in a known area, it is useful as a background for other studies. Thus, it could be used to calibrate more rapid census techniques. We have used it to measure numerical responses of several species to an outbreak of spruce budworm (*Christoneura fumiferana*) (Table 2) and as a background for removal and behavioral experiments (Falls and Loncke, MS; Falls and Brooks 1975).

(9) Combined with individual marking (or recording), playback censuses can be used to mea-

sure population turnover. This may be important, for example, in studies of environmental impacts, where rapid replacement of birds could mask effects if observational census methods were used before and after treatments.

(10) Like other census methods, mapping by playback must be carefully done by an experienced investigator to obtain accurate results. In particular, knowledge of the social structure of populations and the response behavior of each species is important.

Clearly, the methods described here should be tested on more species.

ACKNOWLEDGMENTS

Robert Walker, John Madore and other students assisted with field work. Peter Marler made helpful suggestions about the manuscript. The Ontario Ministry of Natural Resources provided facilities in Algonquin Park. Financial support was provided in part by the National Research Council of Canada.